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A dynamical systems analysis of vertical transmission in host-microbe models

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1 Introduction

Microbes are small organisms that can live in association with a host organism and can impact the host's health. Microbes can be classified in relation to the host as follows: microbes that benefit the host survival are mutualistic, while microbes that are detrimental to the host survival are pathogenic. The host's long term survival, life history, and evolution is often impacted by the presence of microbes, and the microbes' survival is dependent on the continued existence of the host. As such, the complex system of a host and its microbes can be considered one dynamic ecological unit: a holobiont (Thompson et al. (2015)). The interaction between hosts and microbes can be understood using dynamical systems modeling, where microbes have have dynamics on dynamic hosts.

A recent study from Gibbs et al. (2026) used a system of ordinary differential equations to model interactions between a host, pathogenic microbes, and mutualist microbes. Its motivation was to expand the classic competition-colonization tradeoff model to microbes on a dynamic host (namely coral, but the model is not species-specific). Based on the findings of Wang et al. (2022), they chose to model the pathogen as the superior competitor and the mutualist as the superior colonizer. The study assumes that a pathogen may increase a host's death rate and a mutualist may increase a host's colonization rate. One key finding of the study include that the pathogen's ability to kill its host can actually improve coexistence outcomes of all species, but if this effect is too strong, then the pathogen will drive itself to extinction via killing its host. Additionally, mutualist-enhanced growth of the host population can promote coexistence, but this coexistence lead to more complex dynamics – namely limit cycles.

Hosts can acquire microbes by two major routes: horizontal transmission, where microbes are acquired from the environment, or vertical transmission, where microbes are passed down from parent to offspring. This model assumes that the host acquires microbes only via horizontal transmission, leaving questions unanswered about the impacts of vertical transmission. Vertical transmission could be helpful for the host if mutualistic microbes are passed down, but harmful if pathogens are passed down. We aim to investigate how the introduction of vertical transmission impacts host-microbe coexistence outcomes by building off of this original competition-colonization model.

2 Progress

To develop the model, we consider a proportion of a landscape that can be occupied by a host h, where patches on the landscape can either be occupied or empty. When a patch is occupied by a host, it can additionally be colonized by either a mutualist m or a pathogen p. Since microbes require a host to survive, $p + m \leq h$. Hosts spread to unoccupied patches at rate c_h, where the expression $(1 - h)$ represents the uncolonized proportion of the landscape. When occupied by a mutualist, the host can have an elevated colonization rate, c_{hm}. Hosts have an intrinsic death rate d_h and an additional death rate when occupied by a pathogen, d_{hp}. Pathogens spread to hosts unoccupied by itself at rate c_p and have an intrinsic death rate d_p. When hosts carrying a pathogen die, so does the pathogen, so both the d_h and d_{hp} terms enter the pathogen population's rate of change equation. When hosts are born, they have a chance to carry the pathogen with them, so an additional term is added to the equation for p, where the term v_p, between 0 and 1, modifies the pathogen birth rate. Mutualists spread to hosts unoccupied by any bacteria at rate c_m and have an intrinsic death rate d_m. When hosts carrying a mutualist dies, so does the mutualist, so the term d_h enters the mutualist population equation, and when a pathogen colonizes a hosts occupied by the mutualist the mutualist dies, so the term $c_p p$ representing pathogen births enters the equation. A vertical transmission term v_m also increases mutualist birth rate, in a similar way to p. When both v_m and v_p are set to zero, the equations return the model from the original Gibbs et al. (2026) study.

This model is represented by the following system of ordinary differential equations. Note that while both types of microbe can colonize a previously uncolonized host, the pathogen is the better competitor, as it can also colonize hosts occupied by the mutualist, killing the mutualist. In the ecological competition-colonization model, two species occupying the same resource are often able to coexist if one is the superior competitor and the other is the superior colonizer. This system assumes that pathogens are the superior competitor and mutualists are the superior colonizer.

$$\begin{aligned}
\frac{dh}{dt} &= (c_h(h - m) + c_{hm}m)(1 - h) - (d_h h + d_{hp}p) \\
\frac{dp}{dt} &= c_p(h - p)p - (d_p + d_h + d_{hp})p + v_p c_h(1 - h)p \\
\frac{dm}{dt} &= c_m(h - p - m)m - (d_h + c_p p + d_h)m + v_m c_{hm}(1 - h)m.
\end{aligned}$$

Solving the system of differential equations, we observed three different types of long term dynamic behaviors: a not feasible regime, where one or more of the populations dies (goes to 0), a feasible and stable regime, where all three populations coexist at a fixed equilibrium point, and a feasible but unstable regime, where the populations each cycle show limit cycles around an equilibrium point (Otto and Day (2007a)). An example of the feasible but unstable regime is shown in the left-most time series plot in Figure 1B, and an example of the feasible and unstable regime is shown in the right-most time series plot in Figure 1B. To assess the feasibility of a solution we checked for real-valued and positive equilibrium points of the system, and to assess the stability of a solution we checked the Jacobian for negative eigenvalues. Although unstable equilibria could lead to other behaviors such as repelling or neutral limit cycles, we did not observe this in simulations and thus did not consider them.

To begin the investigation on the impacts of vertical transmission, we decided to simplify the system by setting $v_p = v_m$ to reduce the number of changing parameters. In the previous work with the model that considered horizontal transmission only ($v_p = v_m = 0$), the introduction of a mutualist-induced host colonization (c_{hm}) term produced a distinct region of feasible but unstable solutions, shown in the orange region on the left-most bifurcation diagram in Figure 1A. We hypothesized that adding vertical transmission to the system would increase the total area of feasible and stable solutions by stabilizing the cycles. Figure 1A compares the resulting bifurcation diagrams when $v_p = v_m$ is increased from 0, confirming the hypothesis. Not only did feasible and unstable areas stabilize (parts of the previously orange regions turned teal), but previously not feasible areas became feasible (brown regions turned orange), widening the space of possible coexistence for the system. By introducing even small rates of vertical transmission, the proportion of the parameter space ($c_{hm} - c_h$ plane) that permits coexistence of all three species expands. Figure 1B shows a time series plots of one such $c_{hm} - c_h$ coordinate, plotted in red on 1A, which originally displays instability but has dampened oscillations with the introduction of vertical transmission.

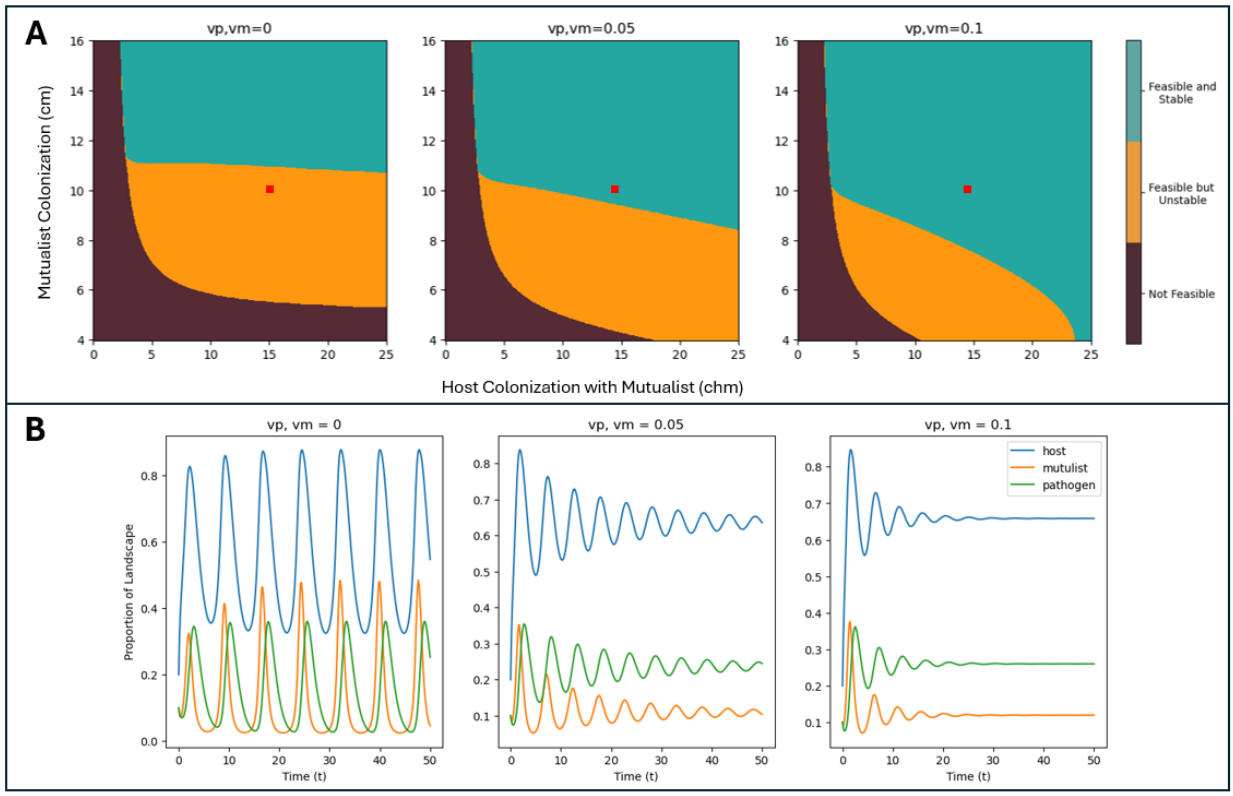

Figure 1: (A) **Increasing vertical transmission alters feasibility outcomes**. Each panel represents a bifurcation diagram as we vary host colonization with mutualist rate c_{hm} (horizontal axis) and mutualist colonization rate c_m (vertical axis). For a given $c_{hm} - c_m$ coordinate, the color of the respective point denotes the analytically derived feasibility of the equilibrium. The red square marks the coordinate corresponding to the time series plots of (B). (B) **Time series diagrams of the points marked in (A)**. The proportion of the host is donated as the blue line, the proportion of the mutualist is denoted as the orange line, and the proportion of the pathogen is denoted as the green line. (Parameters: $c_m = 10, c_p = 5, c_h = 0.25, d_m = 1, d_p = 1, d_h = 1, c_{hm} = 15, d_{hp} = 0$)

While the results presented in Figure 1 may be interpreted to mean that vertical transmission increases potential coexistence situations for all three populations, further investigation complicates this observation. Figure 2 shows a similar bifurcation analysis for varying pathogen colonization (c_p) against mutualist colonization (c_m) for varying v values when no added host colonization from mutualist (c_{hm}) is present. In this case, as v is increased from 0 to 1, $c_p - c_m$ parameter space of feasible solutions shrinks in size. Adding vertical transmission to the system effectively increases the birth rate of the pathogen. Vertical transmission $v_p = v_m$ also increases the birth rate of the mutualist in a similar manner, but the pathogen is the better competitor. From this, the increased pathogen births have a greater chance of spreading further as time goes on, which will often outcompete the mutualist. However, when mutualist colonization rate is sufficiently high, it is still able to coexist with the pathogen, observed in the top left corner of all plots in Figure 2 remains feasible and stable.

One last aspect of the introduction of vertical transmission to the model to be studied was the impact of initial condition on the long term feasibility of the coexistence of the host, the pathogen, and the mutualist. To this end, an additional bifurcation was studied when the initial proportion of the landscape occupied by the host and the mutualist were varied against each other for a constant and small initial condition of the pathogen. Figure 3 displays these results, comparing the model with no vertical transmission against the model with a small amount of vertical transmission. In this case, when vertical transmission was introduced, the amount of the initial condition parameter space that produced long term coexistence of

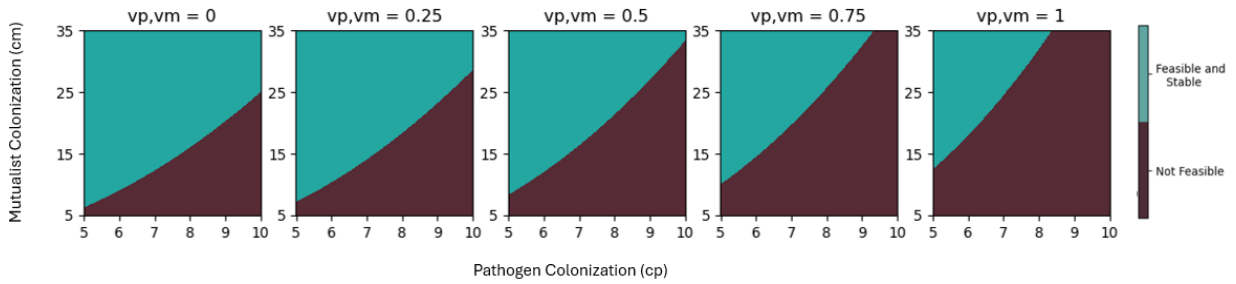

Figure 2: **Bifurcation diagram for varying pathogen colonization c_p against mutualist colonization c_m for different values of $v_p = v_m$.** For a given $c_p - c_m$ coordinate, the color of the respective point denotes the analytically derived feasibility of the equilibrium. Note how the area of the plot that is denoted to be feasible and stable decreases as the v_p and v_m values increase. (Parameters: $c_h = 2, d_m = 1, d_p = 1, d_h = 1, c_{hm} = c_h, d_{hp} = 0$)

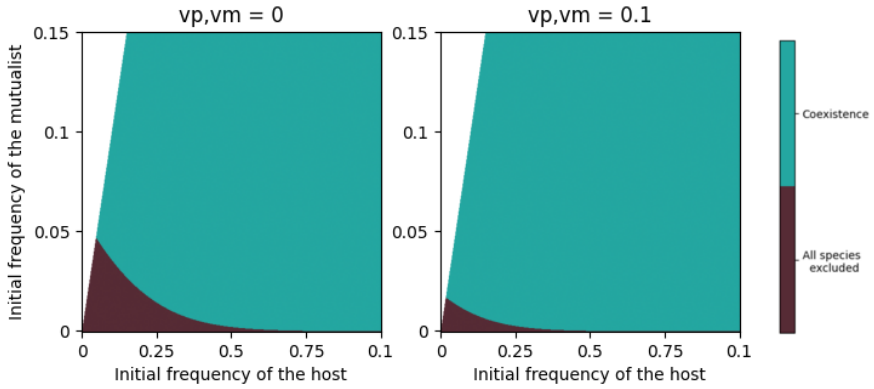

Figure 3: **Bifurcation diagram for varying initial frequencies of the host h_0 and mutualist m_0 at $v_p = v_m = 0$ and $v_p = v_m = 0.1$.** Note that scenarios with $h_0 < m_0$ are not considered, since the mutualist requires the host to survive. For a given $h_0 - m_0$ coordinate, the color of the respective point denotes the analytically derived feasibility of the equilibrium. (Parameters: $c_m = 10, c_p = 5, c_h = 0.5, d_m = 1, d_p = 1, d_h = 1, c_{hm} = 10, d_{hp} = 0$. The initial condition of the pathogen p_0 was set to be $5 \cdot 10^{-5}$)

all three populations expanded. As discussed previously, vertical transmission serves to benefit the birth rate of the mutualist and the pathogen, so smaller initial proportions are thus more likely to be able to gain a foothold in the system and persist over time when vertical transmission is added.

So far, we have set $v_p = v_m$, and explored how the host's vertical transmission of microbes affects the system. However, it may be possible in real-world systems for each microbe to have differing success of vertical transmission. To explore this possibility, we allowed v_p and v_m to differ.

On the diagonal of Figure 4, we see the dampening of oscillations as observed previously for $v_p = v_m$. When $v_m > v_p$, the dampening effect is stronger, and a stable equilibrium is reached even faster with slightly higher proportions of each species as compared to $v_m = v_p$ cases. When $v_p > v_m = 0.1$, the oscillations are not dampened as strongly. We can see that, although the amplitude of oscillations is decaying, when $v_p = 0.5$, each population is still oscillating at the last time point, whereas in the case of $v_p = v_m = 0.1$, the oscillations are nearly undetectable. When $v_m = 0$, increasing v_p appears to increase the amplitude of oscillations instead of reducing them. Increasing v_p to 0.5 causes the otherwise feasible scenario to lead to the death of all three species. Adding v_p without v_m disproportionately increases the effective birth rate of the pathogen via the host, helping to increase its overall proportion of landscape covered. Given that the pathogen out-competes the mutualist and can induce death of the host (d_{hp}), if too much of the host is occupied by the pathogen, the pathogen can then drive both the mutualist and the host to extinction. Since

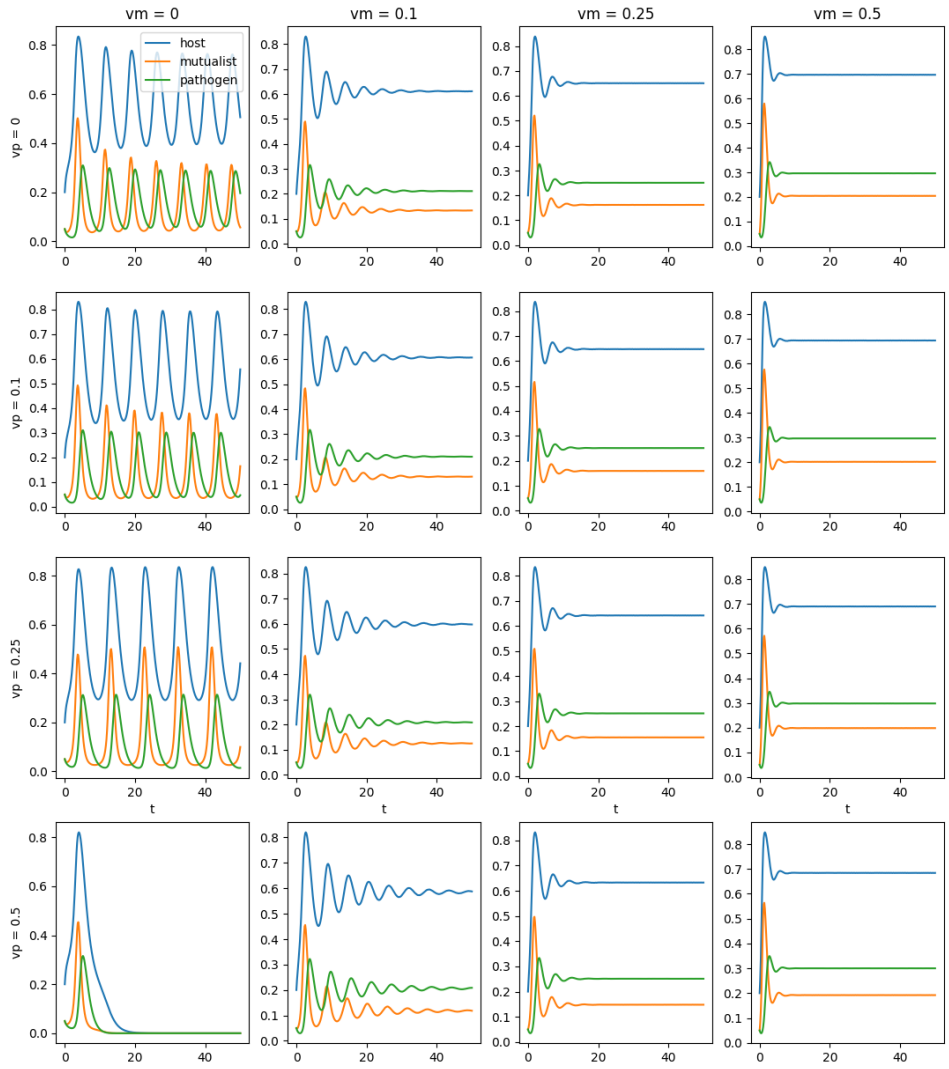

Figure 4: **Time series diagrams with varying levels of vertical transmission**. Each panel represents the frequencies of populations over time for a pair of v_p, v_m, each at values $(0, 0.1, 0.25, 0.5)$. (Parameters: $c_m = 10, c_p = 5, c_h = 0.5, d_m = 1, d_p = 1, d_h = 1, c_{hm} = 10$)

the microbes require the host, both the pathogen and mutualist will die without the host. In this specific parameter set, $d_h = 1 > c_h = 0.5$, so without the added benefit of the mutualist, the host dies at a faster rate than it can colonize landscape, thus dying without the mutualist.

3 Future Plans

While Figure 4 demonstrates our cursory investigation on the qualitatively differential effects of v_p and v_m on the system, moving forward, it would be interesting to quantify these differences. We noticed that for the given set of parameters and initial conditions, it seemed as though v_p increased instability while v_m stabilized the system. However, we don't know whether this holds for other sets of parameter values.

Vertical transmission is a trait of the host species. We could assume that for a given host population, their vertical transmission values v_p and v_m have evolved to some consistent level. If these values are evolutionarily stable, then a mutant host should have a lower fitness than the original host. We could explore whether such an evolutionary stable trait exists, as discussed by Otto and Day (2007b). If so, what

specific parameter values for vertical transmission are evolutionarily stable? Further work could also include discovering whether these dynamics are this reflected in real-life host-microbe systems.

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